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Cryptomeric inheritance in *Onagra**

C. STUART GAGER

(WITH PLATES 20 AND 21)

In a previous publication⁵ I have described an abnormal plant of *Onagra biennis* that appeared in the experimental plot of the New York Botanical Garden in a pedigreed culture following exposure to radium rays. The seed that produced the plant developed in an ovary exposed, before pollination, for 24 hours to the β and γ rays from radium bromid of 10,000 activity contained in a sealed glass tube. After this exposure the stigma was pollinated with unexposed, and, so far as known, normal pollen from another pedigreed individual of *O. biennis*. As described in the paper above cited, the seed gave rise to a plant that produced two shoot systems of equivalent value; that is, neither could be regarded as the main axis of which the other was a lateral branch. Apparently each half of the shoot was from a bud axillary in a cotyledon. Thus it was held that the anomaly was not a bud sport, in the ordinary sense of the word, "unless, keeping in mind that the plumule is a bud, we decide that there was an early bifurcation of the developing embryo, of such a nature that, after the cotyledons were laid down, there was a division of the growing point, accompanied by a separating out of antagonistic characters, and resulting in the formation of two morphologically as well as physiologically different shoots."

Each half of the seedling (15a of my cultures) developed in the usual way, forming a rosette in the seed pan, and subsequently, when planted out, sending up a cauline stem from the center of each rosette.

Taxonomic descriptions of the two plants are here repeated from the former paper,[†] and also an illustration of the young seedling (FIG. 1).

* Brooklyn Botanic Garden: Contributions No. 3.

† Loc. cit. 251.

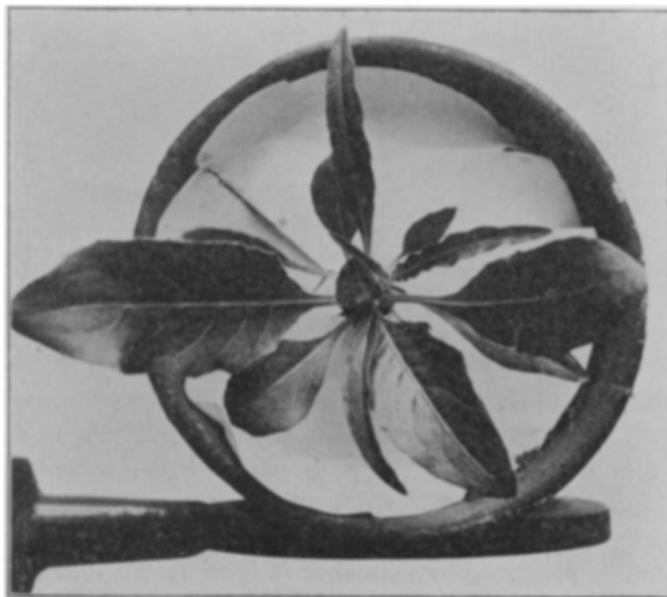


FIG. 1. *Onagra biennis*. Radium culture, no. 15a. Two rosettes, one narrow-leaved and one broad-leaved, on one taproot. Cf. FIG. 2, and PLATES 20 and 21.

15a broad

Rosette leaves finely and sparingly pubescent, the larger ones about 15 cm. long; blades spatulate to elliptic-spatulate, sinuate-dentate especially below the middle, often sharply or prominently so near the base, much longer than the petioles; stem 7 dm. tall, with elongate ascending branches on the lower part; stem leaves mostly spreading; blades narrowly elliptic, somewhat acuminate at the apex, sinuate-dentate; bracts similar to the stem leaves but smaller and usually broadest

15a narrow

Rosette leaves finely and sparingly pubescent, the larger ones 10–12 cm. long; blades almost linear, acuminate at both ends, undulate, somewhat longer than the petioles; stem 6.5 dm. tall, with relatively short ascending branches throughout; stem leaves mostly drooping; blades narrowly linear-lanceolate to almost linear, tapering to both ends, undulate-sinuate; bracts similar to the stem leaves but smaller; hypanthium about 45 mm. long; sepals about 30 mm. long, fully as long as the

below the middle; hypanthium about 35 mm. long; sepals about 25 mm. long, slightly shorter than the free portion of the hypanthium, the free tips in the bud subulate, 2.5–3.5 mm. long; petals about 15 mm. long, nearly truncate at the apex; capsules columnar, slightly narrowed to the apex, about 35 mm. long, much narrower than the bracts.

free portion of the hypanthium, the free tips in the bud long-subulate, 3–4 mm. long; petals about 20 mm. long, nearly truncate at the apex; capsules almost columnar, about 25 mm. long, slightly narrower than the bracts.



FIG. 2. *Onagra biennis*. Radium culture, no. 15a, showing two distinct shoots, morphologically unlike, on one root. The narrow-leaved shoot is at the left. Cf. FIG. 1, and PLATES 20 and 21.

The narrow-leaved branch bore flowers and opening buds for over a week after the broad-leaved branch had ceased to flower, thus pointing to a functional difference. FIGURE 2 shows the mature plant just before anthesis began. The greater vigor of the broad-leaved branch has obscured the equivalency of the two halves, so that the narrow-leaved portion *appears* in FIGURE 2 to be a lateral branch, arising from near the base of the other. Such, however, as pointed out above, was not the case. In PLATES 20 and 21 the morphological features are shown in detail.

Attempts to secure seed from *15a narrow*, either by its own pollen or by crossing it with *15a broad*, were not successful. The broad-leaved branch formed abundant seed when self pollinated, and also when crossed with pollen from *15a narrow*, but in the latter case only one seedling appeared in the seed pan. This plant manifested, throughout, only the characters of *15a broad*, and from it was collected an abundance of close-bred seed, for the purpose of testing whether or not a disjunction of characters would occur. The F₂ generation was grown in the experimental garden of the University of Missouri, at Columbia, Mo. Out of several hundred seedlings, not one showed the characters of the narrow-leaved grandparent, nor did any of these characters appear, either by bud sporting or otherwise, in plants that were allowed to mature.

The following explanations of the original anomaly appear plausible.

1. AN INJURY TO THE ANLAGE OF THE PLUMULE.
2. A QUALITATIVE CHANGE IN EITHER THE EGG OR SPERM that united to form the fertilized egg which gave rise to the plant.
 - a. In the egg, due to exposure to the radium rays.
 - b. In either egg or sperm, spontaneously, or independent of the radium.
3. SECTIONAL BUD-SPORTING IN THE ANLAGE OF THE PLUMULE.
 - a. Due to causes resident in the cells (i. e., spontaneous), and irrespective of the radium rays.
 - (1) The mutation occurred IN THE ANLAGE OF THE PLUMULE.
 - (2) The mutation occurred in one of the germ cells, and the mutated characters first became active as the

plumule developed. This was due either to their separating from the normal characters during nuclear divisions, or to the normal characters becoming inactive.

b. As a result of the previous exposure to radium rays.

Suggestions 1 and 3 (1) above imply, of course, that the anomalous *Onagra* shoot was the expression of merely a somatic change in the plant body, not involving the germ cells at all, and that this is why the atypical characters did not reappear in the generation resulting from a cross between the unlike shoots; or, in other words, that the characters of the narrow-leaved shoot were not represented in the sperm cells of its pollen, and that these gametes were of hereditary content identical with those of the broad-leaved shoot. It is difficult, however, to conceive that such a condition could be realized, since the sperm cells, as truly as all the other cells of the narrow-leaved shoot, are the lineal descendants of the somatic cells which by the supposition were held to have sported. If, however, the characters of the narrow-leaved shoot were due merely to the fact that certain factors that were active in the broad-leaved shoot became inactive in the cell, or group of cells, that give rise to the narrow-leaved shoot, then it is thinkable that these factors became active again in the sperm cells and that thus the original condition was restored. But this does not seem very probable.

A much more probable solution than this emerges from the hypothesis of intracellular pangenesis*: namely, that the change resulting in the narrow-leaved shoot involved only the cytoplasm of the somatic or germ cells concerned, while their nuclei continued to carry, in the inactive state, the original hereditary deposit of the immediate ancestry. Whether the vehicle of this inheritance is conceived of as granular pangens, or as biogens of a definite kind, or as droplets of some enzyme or other chemical substance, or as a relationship merely, between certain bodies, or as any other kind of a "gene," does not affect the hypothesis of a change involving cytoplasm only. In this way an unaltered nuclear germ track might ramify through the plant, resulting in gametes perfectly typical so far as the nucleus is concerned. It is quite probable

* de Vries¹⁶, 197-207.

that we have too much neglected the extra-nuclear cytoplasm in the consideration of the problems of heredity.

Whatever the mechanism of the change is conceived to be, the presumption is in favor of the radium rays as the determining antecedent condition, since such behavior, in the absence of this influence, has never been recorded. But that such a result as the double plant occurred at all is the significant botanical fact; the external "cause" of it is not so important.* Any explanation necessitates the formulation of some definite conception of the structure of protoplasm, and the mechanism of inheritance, and involves the consideration of several working hypotheses already elaborated.

Perhaps the most formal of these hypotheses is that of intracellular pangenes. The essence of this now familiar hypothesis is that all living protoplasm consists entirely of pangens. Pangens are not chemical molecules, but masses of a higher order, having the power of nutrition and growth, of multiplication by division, and of becoming active or latent according to circumstances. When latent they are usually in the nucleus, and become active only when they pass out of the nucleus into the cytoplasm of the cell. These pangens are the bearers of the inheritable unit characters. A change in only the number of pangens causes fluctuating variations; the loss of one or more, or the formation of one or more new kinds of pangens underlies (*is*, in fact) mutation.† As de Vries¹⁷ has stated, this conception formed the basis of the experiments described in his *Mutationstheorie*.

The bearing of this hypothesis on the double primrose-plant is almost too obvious to need stating. We may conceive that all the unit characters which found expression in both the broad-leaved and the narrow-leaved shoot were originally represented in either the egg nucleus or the sperm nucleus‡ that fused in the fertilization. As the fertilized egg developed, they were passed on by nuclear and cell division to all the cells of the embryo; and the apical meristem, at the time the plumule began to be laid down,

* Save as suggesting the possibility of artificially inducing mutative variations by means of radium rays.

† This protoplasmic change is called by de Vries "premutation".

‡ Or both, according to which one of the circumstances above suggested is regarded as the initiation of the change.

became differentiated into two unlike portions. In the cells of one half, the pangens fundamental to the distinguishing characters of the narrow-leaved branch became active, and the pangens fundamental to the distinguishing characters of the broad-leaved branch became latent or wanting. In the cells of the other half the reverse conditions obtained.

From the very nature of the hypothesis of intracellular pangensis, this is, of course, a very formal explanation.

In chapter XIX of my memoir⁵ on Effects of the Rays of Radium on Plants, I have suggested that the effects of the rays may be due to their influence, not directly on the living matter itself, but indirectly, on the enzymes or other non-living inclusions of the cells. This idea of the possible rôle of enzymes in morphogenic changes has been more elaborately worked out by Spillman,¹² who rejects the notion of a supermolecular, organic pangen in favor of, for example, an enzyme acting on some other chemical body, such as a chromogen. "All known Mendelian phenomena," says Spillman,* "may be explained as due to differences in the chemical constitution of the chromosomes in different groups." The failure of a character to appear is attributed to "the failure of a single chromosome to perform a particular function." A practically identical hypothesis was suggested independently by Holmes.¹⁷

Additional evidence that enzymatic action may be involved in mutation is found in the inference, made by de Vries¹⁶ (p. 264), that mutating seeds remain viable longer than non-mutating ones; for it is well known that profound enzymatic changes occur in the aging of dry, resting seeds. Albo's^{1, 2} investigations indicate that the energy for the changes undergone by such seeds is enzymatic in origin, and he states that he was able to demonstrate that diastatic activity was either diminished or entirely wanting in seeds that had lost their capacity to germinate. Dry seeds of many families, and able to germinate, were found by Brocq-Rousseu and Gain³ to contain a peroxydiastase, which the writers claim was never present in seeds that had lost the capacity to germinate. Miss White,¹⁸ however, reports tests on the resting seeds of cereals, showing the presence in them of diastatic, ereptic, and fibrin-digesting enzymes, still active after a period of over

* Loc. cit. 246.

twenty years and after the germinating power of the seeds had been lost. According to Albo, the diastatic power is gradually lost, and it is not at all improbable that the decomposition products, resulting from the breaking down of some enzyme (or other substance, for that matter), may alter the hereditary content of the nucleus, in a manner similar to that effected by MacDougal^{9,10} by injecting dilute solutions of various substances. This would offer a simple explanation of de Vries's observation, above referred to, that older seeds give a larger percentage of mutation than fresh ones. The accumulation of these disintegration products in the nucleus might inhibit or retard the action of certain enzymes involved in growth and development. Moore¹¹ has already suggested that our methods have heretofore been inadequate in taking account of only the end products of reactions. On the other hand, it is possible that new enzymes may develop and become the active agents in the alteration of the nucleoplasm.

In discussing the manner of origin of an *O. rubricalyx* mutant from an *O. rubrinervis* germ cell, Gates⁶ (loc. cit. 204) dismissed de Vries's conception of pangens as "too formal an assumption to be accorded the dignity of an explanation," yet later on (ibid. p. 209) he speaks of "a fundamental change in the germ-plasm," without suggesting how we are to picture this "fundamental change." The rejected theory of de Vries is that of a fundamental change, only the fundament involved is clearly conceived and named by its author. It is difficult to understand how pangens are more "formal" than molecules, and it does not seem to the writer that the "formality" of the hypothesis is a priori a valid reason for rejecting it. It is merely a question of, first, does it agree with known facts, and, second, is there any actual evidence that such bodies as pangens really exist? The recent work of Strasburger¹⁵ seems to indicate that there is, and the facts of development and heredity are such as would follow on the basis of pangenesis.

I do not wish to appear as arguing in favor of intracellular pangenesis as an expression of ascertained truth. On the contrary, I am rather inclined to think that it will have to be either rejected or profoundly modified when the truth is known, if it shall ever be known; but rejected, not because it is formal, but for lack of agreement with observed facts.

Lillie⁸ has recently held that all hypotheses involving the existence of determinants or character units have served their time, and, referring to the work of Guyer and Montgomery, has emphasized the fact that germ-cell elements (chromosomes) may be segregated in nuclear and cell division. This, of course, is well known, and experiments on the effects of radium rays on nuclear division have shown that normal segregation may be greatly altered, and that even elimination of chromatin may be artificially induced in this way.*

I conceive it as quite probable that in the primordium of the epicotyl of the double primrose-plant such a segregation of chromatin material (possibly not entire chromosomes) occurred, accompanying or inducing the organization of two growing points, each the primordium of an epicotyl, and possessing an unlike relation between the hereditary elements of the cells. Not, necessarily, an unlike hereditary composition, for the characters unfolded in the F_1 and F_2 generations showed clearly enough that the characters of an organism that actually appear are a function—not alone of the inheritance of the cells, but of a relation that obtains between various inheritances, some being dominant, others recessive. The work of de Vries has clearly demonstrated that “hereditary potentialities” which exclude each other in the active state, may occur together when one or both are latent.

A qualitatively different chromatin content in the cells of the two growing points may have been the cause of the development of certain enzymes normally absent, or the repression of other ferments ordinarily present. Or these chromatin differences may have given some ferment a suitable body to act on in the one case and not in the other. Since such things as enzymes and fermentable substances are known to exist in plant cells it does indeed seem unnecessary to call in the assistance of an imaginary, new kind of body, until the ones already actually experienced have been shown to be inadequate.

Certain it is, however, as the rich mass of illustrations brought together by Darwin and by de Vries has previously emphasized, that the inheritance of a character and its expression are two entirely different things. The appearance of the double *Onagra*,

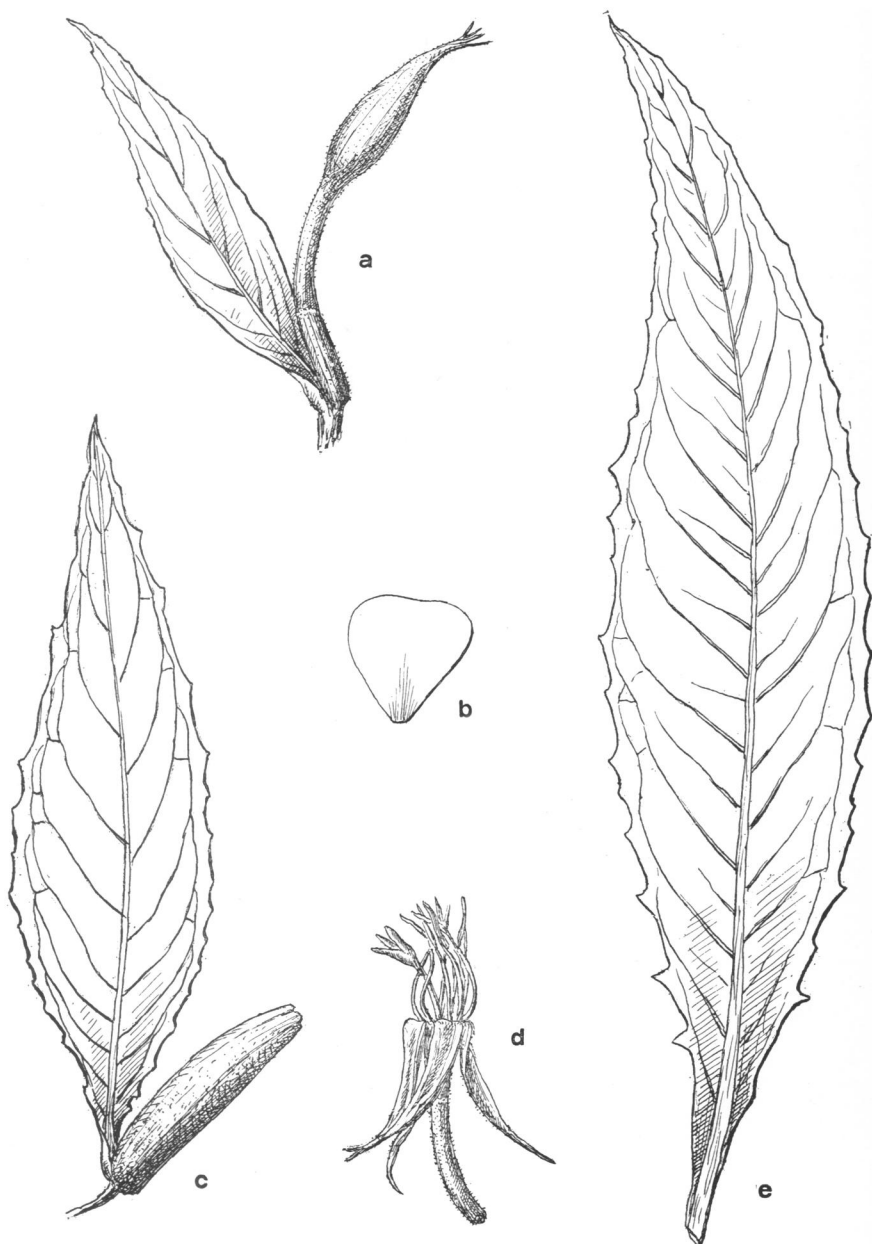
* Gager⁵, Chapt. XVII.

and the character of its first and second filial generations, constitute a striking case in point.

BROOKLYN BOTANIC GARDEN.

BIBLIOGRAPHY

1. **Albo, G.** La vita dei semi allo stato di riposo. Bull. Soc. Bot. Ital. **1907**: 93. 1907.
2. **Albo, G.** Les enzymes et la faculté germinative des graines. Arch. Sci. Phys. Nat. **25**: 45. 1908.
3. **Brocq-Rousseu, & Gain, E.** Sur l'existence d'une peroxydiastase dans les graines sèches. Compt. Rend. Acad. Sci. Paris **145**: 1297. 1907.
4. **Brocq-Rousseu, & Gain, E.** Sur la durée des peroxydiastases des graines. Compt. Rend. Acad. Sci. Paris **146**: 545. 1908.
5. **Gager, C. S.** Effects of the rays of radium on plants. Mem. N. Y. Bot. Gard. **4**: 1-278. 2 D 1908.
6. **Gates, R. R.** The material basis of Mendelian phenomena. Am. Nat. **44**: 203. Ap 1910.
7. **Holmes, S. J.** The categories of variation. Am. Nat. **43**: 257. My 1909.
8. **Lillie, F. R.** The theory of individual development. Pop. Sci. Mo. **75**: 239. S 1909.
9. **MacDougal, D. T.** Heredity, and the origin of species 1-32. Open Court Pub. Co., Chicago. 1905.
10. **MacDougal, D. T.** Report of the department of botanical research. Fifth Year Book Carnegie Inst. 119-135. *pl.* 8-12. Washington, 1907.
11. **Moore, A. R.** A biochemical conception of dominance. Univ. Calif. Publ. Physiol. **4**: 9. S 1910.
12. **Spillman, W. J.** The nature of "unit" characters. Am. Nat. **43**: 243. Ap 1909.
13. **Spillman, W. J.** The Mendelian view of melanin formation. Am. Nat. **44**: 116. F 1910.
14. **Spillman, W. J.** Mendelian phenomena without de Vriesian theory. Am. Nat. **44**: 214. Ap 1910.
15. **Strasburger, E.** Typische und allotypische Kerntheilung. Jahrb. Wiss. Bot. **42**: 1-71. 1905.



GAGER: *ONAGRA BIENNIS*, 15A BROAD



GAGER: ONAGRA BIENNIS, 15A NARROW

16. **Vries, H. de.** The mutation theory. Eng. trans. by Farmer and Darbishire. Vol. I. Chicago, 1909.
17. **Vries, H. de.** Intracellular pangenesis. Eng. trans. by C. S. Gager. Chicago, 1910.
18. **White, J.** The ferments and latent life of resting seeds. Proc. Roy. Soc. London. Ser. B. **81**: 417. 1909.

Explanation of plates 20 and 21

PLATE 20

Onagra biennis. Radium culture, no. 15a, broad leaf. The stigma was pollinated with pollen unexposed to radium rays after the ovary had been exposed for 24 hours to rays from radium bromid of 10,000 activity in a sealed glass tube.

FIG. *a*, flower bud, with bract, taken from a lateral branch; *b*, petal; *c*, nearly mature capsule, with bract (main stem); *d*, flower (minus corolla); *e*, leaf from main stem. Cf. PLATE 21, and FIG. 1 and 2.

PLATE 21

Onagra biennis. Radium culture, no. 15a, narrow leaf. For exposure to radium rays see legend of PLATE 20.